STUDIES IN THE HELIANTHEAE (ASTERACEAE). XVIII.

A NEW GENUS *HELIANTHOPSIS*.

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Though the genus *Helianthus* L. was the first one proposed of those now placed in the subtribe Helianthinae, the genus was never broadly interpreted, and the concept was soon mostly restricted to a natural group of herbaceous species native to North America. Most of the closely related elements in the Neotropics have been placed in such genera as *Simsia* Pers. or in the broadly circumscribed *Viguiera* H.B.K. Nevertheless, a distinctive group of shrubby species from the Andes of Ecuador and Peru, having a deciduous pappus like that of typical *Helianthus*, has continued to be included in the genus. Continuing studies of the Andean Heliantheae have shown the need to treat the disjunct group as a separate genus which is named here as *Helianthopsis*.

The present action rests on two basic conclusions, first, that the Andean group is not directly related to typical *Helianthus* of North America, and second, that it should not be included in a further broadened concept of the genus *Viguiera*. Actually, the problem of a polyphyletic *Helianthus* has been clearly stated for many years. Heiser (1957), in his study of South American *Helianthus*, concluded that *Viguiera* was the likely ancestral genus in the complex and that the two elements of *Helianthus* were separately derived. The deciduous pappus with obsolete squamellae in *Helianthus* versus a persistent pappus with prominent squamellae in *Viguiera* was the only difference then recognized for separating the genera, but Heiser argued against reducing *Viguiera* into synonymy in order to restore a phyletic concept. Nevertheless, Heiser did nothing more with the South American *Helianthus* than to rather informally propose a new subgenus, *Viguieropsis*, distinguished from the North American species by the shrubby habit.

An important character is now known which confirms the polyphyletic nature of *Helianthus*. The styles of the South American species have short tips without an appendage. The North American species have a long slender appendage present on the point of the style, a feature evident in even those species that have become cultivated or established in South America. In reality, typical *Helianthus* seems to find its closest relative in the genus *Simsia*, which also has a slender style appendage (Robinson & Brettell, 1972), but which has generally slender style branches which often coil when dried. It is significant

that typical Viguiera also possesses a short but distinct appendage on its style (Robinson, 1977), and future trends will almost certainly require a narrowing rather than a broadening of that genus.

The present generic delimitation of Helianthopsis follows what has been called Helianthus in the Andes, and though the traditional separation from Viguiera is thus maintained, some clarification is necessary. In spite of the evident close relation of Helianthopsis with Andean elements presently placed in Viguiera, the division does seem to be a natural one. In Helianthopsis, the species that show superficial resemblance to Viguiera are all members of the specialized pale-anthered group. The less shrubby scarcely tomentose H. matthewsii would not immediately be recognized as a member of the genus, but it has the typical pappus form. Helianthopsis hutchisonii actually has a Viguiera-type pappus but has leaf pubescence, head structure and anther color which indicate its place in the pale-anthered series remote from anything in Viguiera. In Viguiera, only V. sodiroi (Hieron.) Blake and some specimens of V. incana (Pers.) Blake are likely to be mistaken for Helianthopsis because of the presence of tomentum, but they are perennial herbs, they have an obvious Viguiera-type pappus, and they are much like other species of Andean Viguiera in the way the lower lateral veins run subparallel to the leaf margin. The leaves and stems of both species tend to have at least some coarser pubescence unlike that of Helianthopsis.

Other generic names that have been used for Andean Helianthinae with exappendiculate styles are Leighia Cass. and Syncretocarpus Blake. Leighia originally included Helianthopsis microphylla, but the type was the herbaceous Mexican species, L. elegans Cass. (= Viguiera linearis (Cav.) Sch.Bip., Blake 1918). Syncretocarpus was established for a group of Peruvian species. The characteristic margin on the achene of Syncretocarpus was simply a differentiated zone rather than a Verbesina-type wing as suggested by Blake (1916), and the relationship of the genus is entirely within the Viguiera complex. Still, the suffrutescent habit and well-developed Viguiera-type pappus indicate a position apart from Helianthopsis.

In establishing the new genus, the informally proposed subgenus Viguieropsis has seemed an unlikely candidate for elevation. In any case, the name Helianthopsis seems best as a reflection of the historical placement of the species.

Helianthopsis H.Robinson, genus nov. Asteracearum (Heliantheae).

Plantae frutescentes mediocriter ramosae. Folia opposita vel alterna; laminae ovatae vel anguste oblongae plerumque distincte pubescentes supra dense vel perdense pilosae subtus tomentosae vel lanatae inferne trinervatae, nervis marginem non parallelis. Inflorescentiae terminales pauce capitatae. Squamae involucri plerumque triseriatae in part herbaceae;

paleae subconduplicatae obtusae vel breviter acutae. Flores radii numerosi asexuales; corollae flavae 2-3-lobatae supra papillosae. Flores disci numerosi hermaphroditi; corollae flavae vel superne nigrescentes 5-lobatae, faucis anguste campanulatis inferne plerumque scabridis; filamenta glabra; thecae antherarum plerumque nigrescentes; appendices antherarum abaxialiter glanduliferae et interdum setiferae; rami stylorum obtusi exappendiculati, linis stigmataceis solitariis. Achaenia disci distincte compressa striata; aristae pappi base articulatae facile deciduae; squamellae paucae vel nullae.

Type species: Helianthus microphyllus H.B.K.

Twenty species are presently recognized in the genus. Also, as described, Helianthus argenteus H.B.K., from Azuay in Ecuador, has the characters of Helianthopsis. A photograph of the type shows solitary heads that are sometimes on rather long erect peduncles, a character that is rather unusual for the genus. No material matching the latter species has been seen in the present study, and it is omitted from the listing and key.

The genus is distributed from northern Ecuador southward to central Peru with a major concentration of species in Cajamarca and adjacent areas of northern Peru. In addition, Heiser (1957) cites a specimen of H. imbaburensis from Nariño in southwestern Colombia.

The phytogeographic approach has proven useful in the study of the species concepts, though not as clearly as in the case of Monactis (Robinson, 1976). The break betweem Ecuadorian and Peruvian elements of Helianthopsis is particularly marked, and no species is presently known from both countries. Furthermore, the black-anthered species of Ecuador and Peru seem to form two thoroughly distinct natural groups, and the pale-anthered species of Ecuador are obviously more closely related to each other than to those of Peru. The center of diversity is evidently in Peru with only the H. lehmannii group being restricted to Ecuador. No species with reflexed palea tips are known from Ecuador, though the character is seen in both black-anthered and pale-anthered species from Peru. Opposite leaves are found in many Peruvian species including some that are primarily alternate such as H. stuebelii and H. sagasteguii, the latter being one of the pale-anthered species. No opposite leaves have been seen in any specimens from Ecuador. In both H. lehmennii and H. grandiceps of Ecuador the anther appendages apparently vary in color from yellow to black. In Peruvian species, with the possible exception of H. discolor, the color of the anther appendages seems to be a reliable species character.

The following key attempts to de-emphasize use of opposite versus alternate leaves since the character is evidently variable and is poorly represented in many specimens.

Key to the species of Helianthopsis

1. Anther thecae at maturity not black. Most involucral bracts with prominent pale costae below and herbaceous distally. Disk corolla never black distally. Heads not solitary.

2. Ecuadorian species. Tips of paleae never recurved. Heads often densely clustered.

3. Leaves lanceolate, entire or slightly serrulate above H. pseudoverbesinoides

3. Leaves mostly ovate, serrulate or serrate mostly at widest part of blade.

4. Outer involucral bracts with distinctly reflexed tips H. hypargyrea

4. Outer involucral bracts without reflexed tips H. imbaburensis

2. Peruvian species. Tips of paleae often recurved. Heads usually laxly disposed.

5. Heads with disk mostly 5-7 mm wide. Corolla lobes scarcely emergent beyond paleae.

6. Leaves ovate-lanceolate, not much reduced in inflorescence, not more densely pubescent below H. matthewsii

6. Leaves narrowly lanceolate, reduced in inflorescence, obviously tomentose below H. verbesinoides

5. Heads with disk mostly 10-15 mm wide. Mature corollas with upper throat emergent beyond paleae.

7. Leaves lanceolate, entire, reduced in inflorescence. Stems puberulous H. hutchisonii

7. Leaves broadly ovate, serrate, moderately reduced in inflorescence. Stems hirsute H. sagasteguii

1. Anther thecae black at maturity. Outer involucral bracts without distinct pale costae basally. Disk corolla yellow or distally blackened.

8. Ecuadorian species. Leaves alternate; with blades large, often to 9-10 cm long and 5-7 cm wide, margins never reflexed; paleae glabrous on outer surface.

9. Peduncles and involucres densely lanate. Corolla lobes longer than wide, nearly glabrous on outer surface H. lehmannii

9. Peduncles hirsute with interspersed shorter hairs visible. corolla lobes equilaterallly triangular, densely pubescent on outer surface.

10. Numerous outer involucral bracts with reflexed narrow tips, mostly greenish H. grandiceps

10. Few or no differentiated outer involucral bracts, tips obtuse to short-acute, involucre blackish with outer surfaces sometimes partly subglabrous H. nigrescens

8. Peruvian species. Leaves alternate or opposite; blades often small, never more than 7 cm long or 4.5 cm wide. margins often reflexed; paleae usually pubescent on outer surface.

11. Anther appendages completely black. Leaf blades ovate or broadly oblong.

12. Stems and undersurfaces of leaves white-lanate. Paleae narrowly pointed and strongly recurved at tip H. lanata

12. Stems and undersurfaces of leaves mostly tomentose, usually yellowish or dingy white. Paleae sharply acute and erect to slightly recurved at tip H. stuebelii

11. Anther appendages partly to completely yellow.

13. Paleae all with sharply reflexed tips. Leaves ovate to broadly ovate H. senex

13. Paleae with tips erect or incurved, rarely reflexed.

14. Leaves densely puberulous or short-pilose below, pubescence not covering surface H. viridior

14. Leaves distinctly tomentose or lanate below.

15. Leaf blades ovate.

16. Leaf tips distinctly acuminate or narrowly acute. Heads raised on distinct peduncles. Rays with styles present H. acuminata

16. Leaf tips short-acute to obtuse. Heads short-peduncculate or subsessile. Rays without styles.

17. Leaves opposite, petiole 10-20 mm long H. jelskii

17. Leaves mostly alternate, petiole 3-5 mm long H. lodicata

15. Leaf blades narrowly oblong to linear or linear-lanceolate.

18. Stems mostly puberulous. Heads solitary on tips of slender branches; anther appendages often partially blackened; tips of a few paleae reflexed H. discolor

18. Stems densely lanate. Heads usually more than 1 on tips of branches; anther appendages yellow; tips of paleae all erect or incurved.

19. Upper leaf surface subglaucous with very dense very minute puberulence, surface not rugulose. Heads distinctly pedunculate on branches with some reduced leaves H. microphylla

19. Upper leaf surface coarsely puberulous, somewhat rugulose. Heads short-pedunculate or subsessile, clustered at tips of normally leaved branches H. subnivea

The twenty recognized species of Helianthopsis are as follows.

Helianthopsis acuminata (Blake) H.Robinson, comb. nov. Helianthus acuminatus Blake, Jour. Wash. Acad. Sci. 16: 219. 1926. Peru (Huanuco, Junin). The type and one other specimen (Hutchison 4153) have been seen, the latter differing by the lack of opposite leaves. Both specimens have distinct though probably non-functional styles in the ray flowers, a feature that seems unique in the subtribe.

Helianthopsis discolor (Blake) H.Robinson, comb. nov. Helianthus discolor Blake, Jour. Wash. Acad. Sci. 16: 220. 1926. Peru (Cajamarca, Huanuco, La Libertad). The specimen seen from Cajamarca (Soukup 4548) has sericous pubescence on the leaves and often multiple aristae on the achenes. Also, some of the heads have pale anthers, but the latter heads are apparently defective.

Helianthopsis grandiceps (Blake) H.Robinson, comb. nov. Helianthus grandiceps Blake, Contr. U.S. Nat. Herb. 22: 621. 1924. Ecuador (Azuay, Chimborazo, Loja).

Helianthopsis hutchisonii H.Robinson, sp. nov.
Plantae frutescentes ad 2 m altae inferne pauce vel non

ramosae. Caules purpurascentes inferne dense cinereo-puberuli superne sparse puberuli. Folia alterna, petiolis 3-10 mm longis; laminae ovato-lanceolatae plerumque 4-7 cm longae et 0.7-2.3 cm latae base anguste rotundatae et sensim breviter acuminatae margine integrae apice anguste acutae supra velutinae subtus tenuiter albo-tomentosae fere ad basem trinervatae. Inflorescentiae terminales perlaxe ramosae, ramis elongatis superne tenuibus, bracteis anguste ellipticis vel linearibus 8-20 mm longis et 1-3 mm latis. Capitula hemisphaerica 12-14 mm alta et sine radiis ca. 15 mm lata. Squamae involucri ca. triseriatae ca. 20 anguste oblongae vel lineares 4-9 mm longae et 1.5-3.0 mm latae inferne pallide 2-4-costatae supra medium herbaceae apice acutae extus dense hirtellae intus in partibus herbaceis dense puberulae; paleae oblongo-ovatae ca. 9 mm longae pallide 4-6-costatae margine late scariosae apice acutae distincte reflexae extus minute puberulae. Flores radii ca. 12; corollae flavae 12-13 mm longae et 4 mm latae extus dense minute hispidulae, limbis glanduliferis, tubis 1-2 mm longis. Flores disci ca. 50; corollae flavae ca. 8 mm longae, tubis ca. 1 mm longis subglabris, faucis cylindraceis ca. 6 mm longis extus dense scabridulis et pauce tenuiter glandulo-piliferis, lobis triangularibus ca. 1.0 mm longis et 0.9 mm latis intus valde papillosis extus dense scabridulis; filamenta in parte superiore ca. 0.3 mm longa; thecae antherarum ca. 3 mm longae non nigrescentes; appendices antherarum ovatae ca. 0.45 mm longae et 0.4 mm latae. Achaenia radii sterilia ca. 3 mm longa glabra, squamellae pappi numerosae. Achaenia disci ca. 4.3 mm longa et 1.6 mm lata dense sericeo-setifera; aristae pappi 2 ca. 3.5 mm longae mediocriter deciduae; squamellae pappi 10-12 late lineares ca. 1.5 mm longae subpersistentes. Grana pollinis 35-37 μm in diametro longe spinosa.

TYPE: PERU: Cajamarca: Celendin: Opposite Balsas & upstream 1 km. Common border of Dept. Amazonas, on Rio Marañon. Alt. ca. 800 m. To 2 m. 29 May 1964. P.C.Hutchison & J.K.Wright 5436 (Holotype US, Isotypes F, UC, USM).

Helianthopsis hutchisonii is notable in the genus for the Viguiera-type pappus, a feature that does not seem to reflect any close relationship to species presently placed in Viguiera. Both the leaf-venation and the pubescence is strictly of the Helianthopsis type. In fact, H. hutchisonii is evidently a specialized member of the pale-anthered series of Helianthopsis, and it seems quite close to H. sagasteguii n. sp., having the same type of reflexed tips on the paleae. Differences of the new species include the shorter pubescence on the stems and leaves, the narrower entire leaves and the more open inflorescence with narrow reduced bracts. The new species also seems to occur at lower elevations than other members of the genus.

Helianthopsis hypargyrea (Blake) H.Robinson, comb. nov.
Helianthus hypargyreus Blake, Bot. Gaz. 74: 421. 1922.

Ecuador (Azuay, Chimborazo, Tungurahua).

Helianthopsis imbaburensis (Hieron.) H.Robinson, comb. nov. Helianthus imbaburensis Hieron., Bot. Jahrb. 21: 348. 1895. Ecuador (Imbabura), Colombia (Nariño).

Helianthopsis jelskii (Hieron.) H.Robinson, comb. nov. Helianthus jelskii Hieron., Bot. Jahrb. 36: 490. 1905. Peru (Cajamarca).

Helianthopsis lanata (Heiser) H.Robinson, comb. nov. Helianthus lanatus Heiser. Brittonia 8: 291. 1957. Peru (Ancash, Lima).

Helianthopsis lehmannii (Hieron.) H.Robinson, comb. nov. Helianthus lehmannii Hieron. in Sod., Bot. Jahrb. 29: 39. 1900. Ecuador (Cañar, Chimborazo, Pichincha).

Helianthopsis lodicata (Cuatr.) H.Robinson, comb. nov. Helianthus lodicatus Cuatr., Proc. Biol. Soc. Wash. 77: 144. 1964. Peru (Cajamarca).

Helianthopsis matthewsii (Hochr.) H.Robinson, comb. nov. Helianthus matthewsii Hochr., Bull. N. Y. Bot. Gard. 6: 296. 1910. Peru (Amazonas, Cajamarca).

Helianthopsis microphylla (H.B.K.) H.Robinson, comb. nov. Helianthus microphyllus H.B.K., Nov. Gen. et Sp. ed. fol. 4: 173, pl. 375. 1818. Leighia microphylla Cass., Dict. Sci. Nat. 25: 436. 1822. Viguiera microphylla Hieron., Bot. Jahrb. 36: 490. 1904. Peru (Cajamarca).

Helianthopsis nigrescens (Heiser) H.Robinson, comb. nov. Helianthus nigrescens Heiser, Brittonia 8: 287. 1957. Ecuador (Azuay).

Helianthopsis pseudoverbesinoides (Hieron.) H.Robinson, comb. nov. Helianthus pseudoverbesinoides Hieron. in Sod., Bot. Jahrb. 29: 40. 1900. Ecuador (Bolivar, Chimborazo, Tungurahua).

Helianthopsis sagasteguii H.Robinson sp. nov.

Plantae frutescentes as 2 m altae inferne pauce ramosae in caulibus inflorescentiis petiolis et superficiis superioribus foliorum dense hirtellae vel hirsutae. Caules inferne fuscescentes vel atro-purpurascentes. Folia alterna inferne interdum opposita, petiolis 1-3 cm longis; laminae late ovatae plerumque 5-12 cm longae et 3-9 cm latae base late rotundatae vel subtruncatae ad medium breviter acuminatae margine distincte serratae vel dentatae apice anguste acuminatae supra velutino-hirtellae subtus dense areolate tomentosae fere ad basem valde

trinervatae. Inflorescentiae terminales divaricate ramosae pauce capitatae, ramis ultimis plerumque 2-3 cm longis, bracteis ovatis 1.5-4.5 cm longis et 1.0-3.5 cm latis. Capitula hemisphaerica ca. 12 mm alta et sine radiis ca. 15 mm lata. Squamae involucri ca. triseriatae ca. 20-25 anguste oblongae vel lineares 6-11 mm longae et 2-3 mm latae inferne pallide 2-4-costatae supra medium herbaceae apice argute acutae extus hirtellae intus in partibus herbaceis dense puberulae; paleae oblongo-ovatae 6-7 mm longae pallide 4-6-costatae margine late scariosae apice acutae distincte reflexae extus minute puberulae. Flores radii 12-14; corollae flavae 12-14 mm longae et 4.5 mm latae extus dense hispidulae, limbis glanduliferis, tubis ca. 2 mm longis. Flores disci 65-80; corollae flavae 3.5-6.0 mm longae, tubis 0.7-2.0 mm longis subglabris vel sparse hispidulis, faucis cylindraceis ca. 2-3 mm longis extus dense scabridulis et pauce tenuiter glandulo-piliferis, lobis triangularibus 0.7-1.2 mm longis et 0.6-1.0 mm latis intus superne papillosis extus dense scabridulis; filamenta in parte superiore ca. 0.3 mm longa; thecae antherarum ad 2.3 mm longae non nigrescentes; appendices antherarum ovate ad 0.5 mm longae et 0.4 mm latae. Achaenia radii sterilia ad 2.8 mm longa apice pauce squamulifera. Achaenia disci ad 3.7 mm longa et 1.4 mm lata dense sericeo-setifera vel glabra; aristae pappi 2 plerumque 2.0-2.5 mm longae facile vel mediocriter deciduae; squamellae pappi pauce vel nullas ad 0.8 mm longae. Grana pollinis ca. 30 um in diametro longe spinosa.

TYPE: PERU: Cajamarca: Celendin: Canyon Rio Marañon above Balsas 11 1/2 km below summit of road to Celendin. Shrub to 2 m. Stems, leaves densely puberulent. Rays bright golden. Disks yellow (dull). Aspect of plant silvery. Abundant. Alt. 2630 m. 27 May 1964. P.C.Hutchison & J.K.Wright 5397 (Holotype US, Isotypes F, UC, USM). PARATYPE: PERU: Cajamarca: Celendin: Hda. El Limón (Celendín-Balsas). Alt. 2150 m. ladera de arbustos. Aubarbusto piloso de flores amarillas. 5 May 1970. Sagastegui 7415 (US, HUT).

Helianthopsis sagasteguii is similar to H. hypargyrea in general aspect, and is in the same group having pale anther thecae. However, the two species do not seem to be immediate relatives. The paleae of H. sagasteguii have strongly reflexed tips and the inflorescence is rather lax, two characters of the Peruvian members of the pale-anthered group not found in the species from Ecuador. The new species is the only member of the series presently known to have some opposite leaves, but the specimen is more complete than most. The heads examined show great variation in achene pubescence and pappus structure, but the typical Helianthus-type pappus predominates, and the squamellae, when present, never seem to fill the entire lateral margin.

Helianthopsis senex (Blake) H.Robinson, comb. nov. Helianthus senex Blake, Jour. Wash. Acad. Sci. 16: 220. 1926. Peru

(Huanuco).

Helianthopsis stuebelii (Hieron.) H.Robinson, comb. nov. Helianthus stuebelii Hieron., Bot. Jahrb. 21: 249. 1895. Peru (Cajamarca).

Helianthopsis subnivea (Blake) H.Robinson, comb. nov. Helianthus subniveus Blake, Contr. U.S. Nat. Herb. 22: 621. 1924. Helianthus niveus Hieron., Bot. Jahrb. 21: 350. 1895. not H. niveus Brandegee 1889. Peru (Cajamarca).

Helianthopsis verbesinoides (H.B.K.) H.Robinson, comb. nov. Helianthus verbesinoides H.B.K., Nov. Gen. et Sp. ed. fol. 4: 173. 1818. Peru (Piura).

Helianthopsis viridior (Blake) H.Robinson, comb. nov. Helianthus viridior Blake, Jour. Wash. Acad. Sci. 16: 221. 1926. Peru (Junin).

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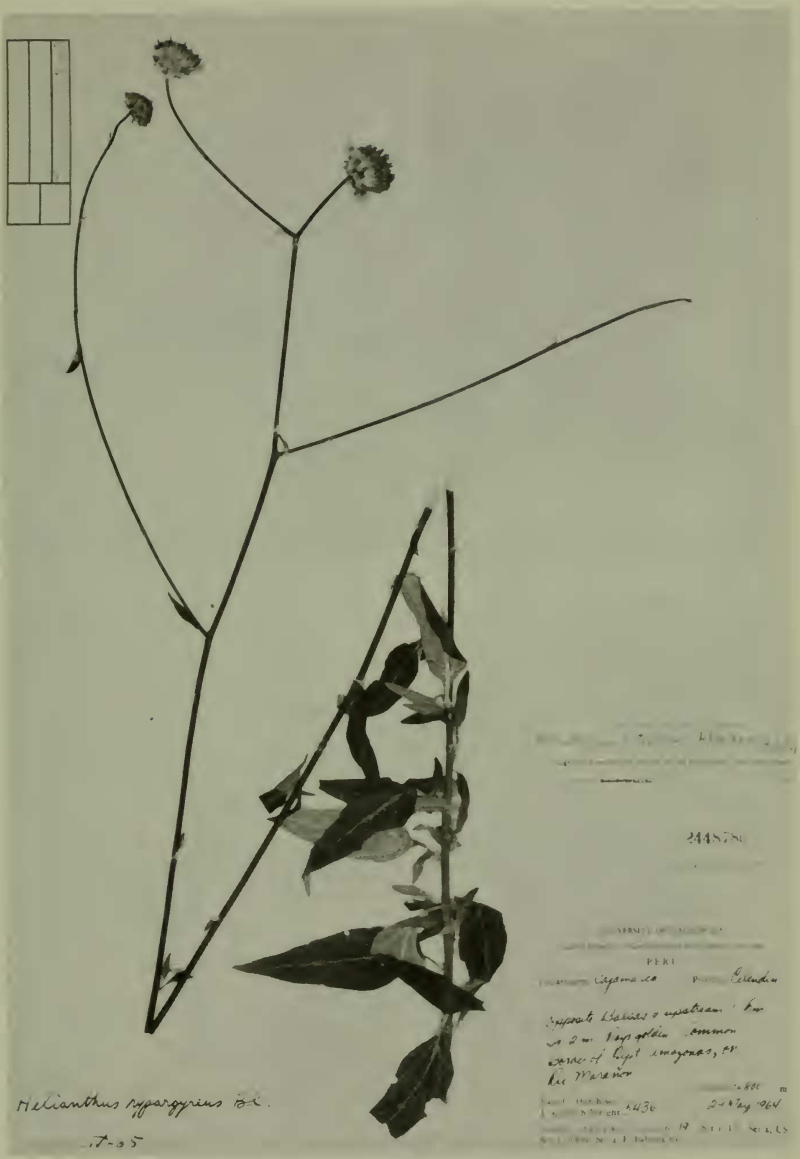
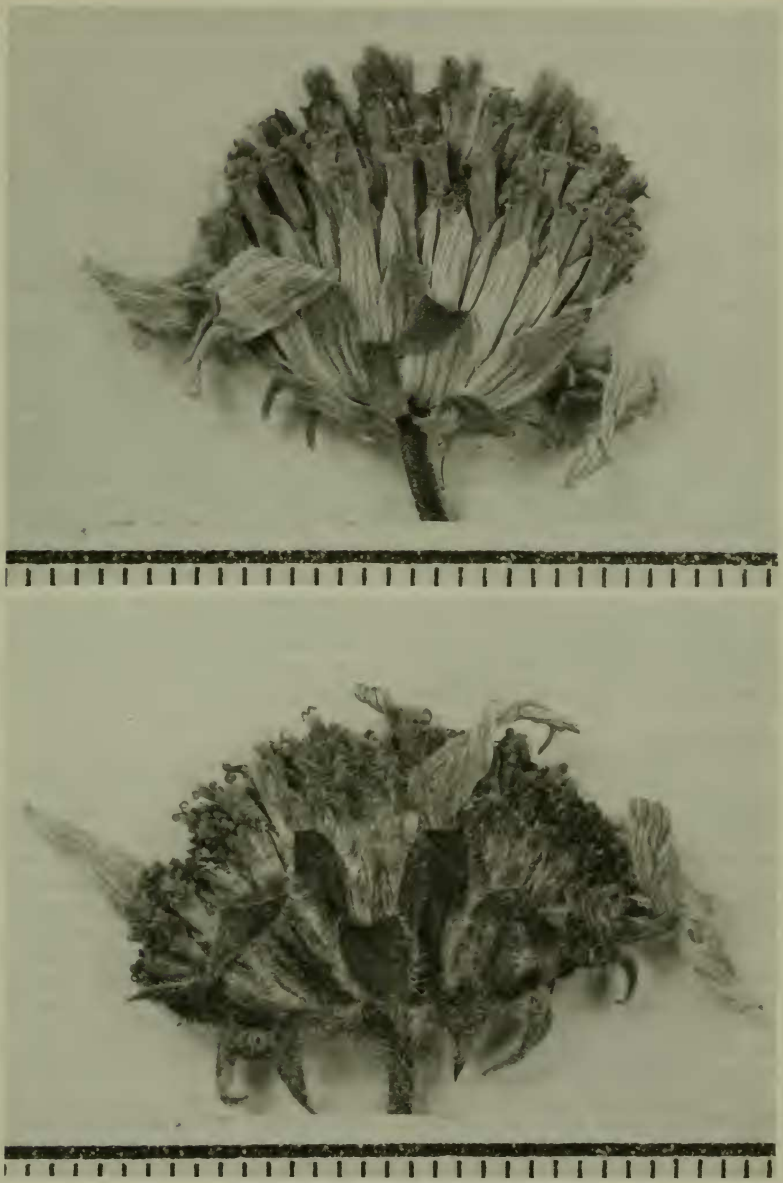


Helianthopsis hutchisonii H.Robinson, Holotype, United States National Herbarium. Photos by Victor E. Krantz, Staff Photographer, National Museum of Natural History.

Helianthopsis sagasteguii H.Robinson, Holotype, United States National Herbarium.



Helianthopsis enlargements of heads: Top. *H. hutchisonii*. Bottom. *H. sagasteguii*.